Modification of Coral Reef Zonation by Terrigenous Sediment Stress

Roberto Acevedo; Jack Morelock; R. A. Olivieri

Stable URL:

http://links.jstor.org/sici?sici=0883-1351%28198902%294%3A1%3C92%3AMOCRZB%3E2.0.CO%3B2-1

Modification of Coral Reef Zonation by Terrigenous Sediment Stress

ROBERTO ACEVEDO,
JACK MORELOCK, and
R.A. OLIVIERI
*Department of Marine Sciences,
University of Puerto Rico,
Mayaguez, PR 00708*

Four coral reefs near Ponce, Puerto Rico were examined for the effects of terrigenous influx into a reef environment. The four coral reefs are successively farther from a point source of frequently occurring, westward-moving terrigenous sediment plumes which are generated by resuspension of fine-grained sediments.

The coral cover was measured from linear photographic transects parallel to each 5 meter depth. Living coral was marked on each photograph, the species identified, and area of cover was measured with a Jandel digitizer pad and SigmaScan program. Statistics were compiled for percent cover by species, total cover, and number of colonies.

Total coral cover was reduced near the source of terrigenous sediment influx. Coral cover and diversity increased with distance from the source and amounts of sediment trapped on the reefs decreased, suggesting that the plume influx was an important factor contributing to the deterioration of these reefs. Sediment stress has drastically reduced the coral cover and number of species. The reefs with high sediment inputs showed decreased coral species diversity and percent cover. Sediment-resistant coral species tolerated this adverse environment and their percent of cover remained relatively constant. The effects from sediment influx include partial or total burial of coral colonies, bleaching, and colonization of the coral surface by filamentous blue-green algae and sponges. The reduced light levels resulted in domination of the community by deeper fore-reef coral.

INTRODUCTION

Abundant coral reefs are present on the east, south, and west coasts of Puerto Rico. The reef types commonly encountered are fringing, barrier shelf, and submerged shelf edge. The offshore reefs are still in good condition, but the environment of much of the nearshore regions of all three coasts has changed to a high terrigenous sediment influx condition with a loss of coral cover accompanied by lack of growth or recolonization of reef areas. Large areas of dead coral on the present reefs show that the reefs were once far more extensive in area. It is commonly accepted that resuspension and deposition of fine terrigenous sediments reduce total coral cover and the number of species. We have measured large areas of reef front in order to quantify these assumptions and to determine which species are more sediment resistant in the natural environment. The process of change in the amount of terrigenous sediment influx and the long-term effects of sediment stress on coral reef systems was examined at four coral reef sites near Ponce, Puerto Rico (Figure 1). The four coral reefs studied are successively farther from a point source of westward-moving terrigenous sediment plumes.

In order to examine changes in the reef-front zonation at Ponce, reefs at La Parguera, Puerto Rico, were also investigated in detail and used as a standard reef zonation pattern for the south coast of Puerto Rico (Fig. 1). The reefs at Parguera are surrounded by coarse-grained carbonate sediments and are free of terrigenous sediment influx (Morelock et al., 1977). No rivers enter the sea along this semi-arid stretch of coastline, and local terrigenous runoff during heavy rains is trapped in the coastal and nearshore mangrove system (pers. obs.). Water transparency is

greater than 10 m Secchi more than 90% of the time (Rogers, 1977).

METHODS

Horizontal photo-transects, consisting of three 15 m chains of eleven 70 × 100 cm area photographs each, were made at each 5 m depth interval down all reef fronts at Ponce and Parguera. Coral identifications were made in the field, and the colonies were tagged for identification on the photographs. Total area examined at each depth level was 23 m^2 over a distance of about 50 m. The living coral was marked on each photograph and the species identified (Fig. 2). Areas were measured with a Jandel digitizer pad and their SigmaScan program. Statistics were compiled for percent cover by species, total coral cover, and number of colonies. From these measurements and prior studies at Parguera, we developed the zonation scheme used as a standard for this study and then measured the changes in total coral cover and cover by species on sediment-impacted reefs.

PARGUERA REEF-FRONT ZONATION

At Parguera, four distinct coral reef zones can be distinguished below the reef crest (Table 1). The community zonation of the reef front is similar to that at Yucatán (Logan, 1969), Jamaica (Goreau and Goreau, 1973), and Belize (James and Ginsburg, 1979). The *Acropora palmata* Zone is restricted to relatively clear waters with moderate to strong wave energy. This zone is absent or is represented by very limited occurrence of *Acropora palmata* in turbid waters, and also is frequently modified by hurricane waves. For these reasons, this zone was not included in this study.

The next depth zone, the Mixed Coral Zone, is dominated by *Montastrea annularis* and *Acropora cervicornis*. The Mixed Coral Zone occupies a fairly level part of the reef front, and is distinguishable mainly because of the effect of a change from steeper slopes found in the other zones. This zone is probably a local feature, related to a Holocene
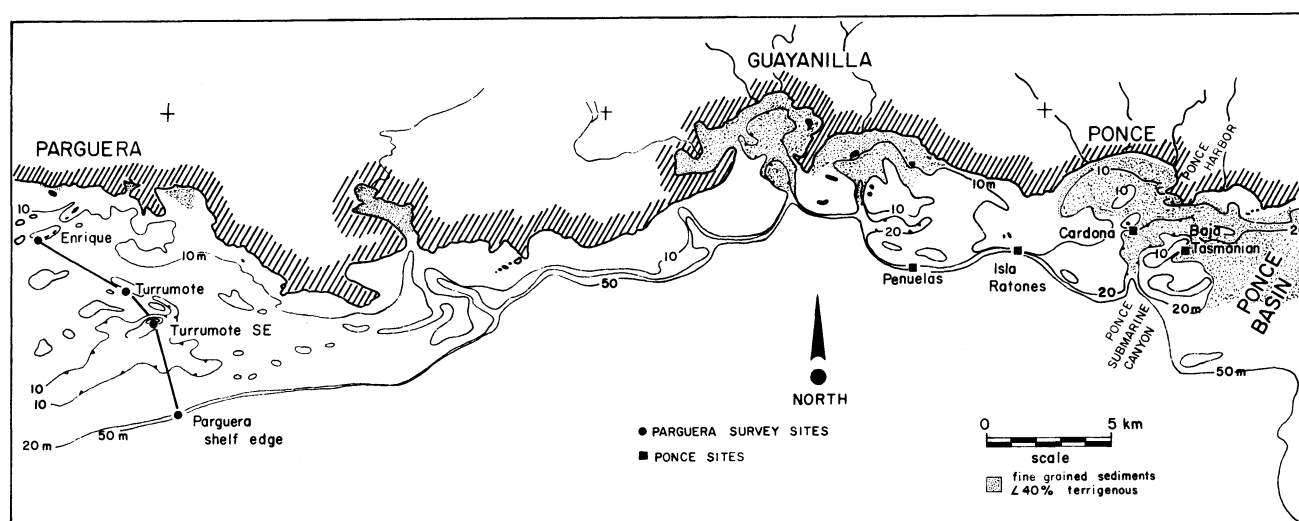
FIGURE 1—Location map for Ponce and Parguera reef surveys, southwest Puerto Rico.

TABLE 1—Parguera coral reef zonation

REEF ZONES	*Acropora palmata*	Mixed Coral Zone	Massive Coral Zone	*Agaricia-Montastrea*
Dominant Species	A. palmata	M. annularis A. cervicornis	M. annularis Diploria	M. annularis Agaricia agaricites
Abundant Species	M. annularis P. asteroides	Porites porites Diploria P. asteroides	M. cavernosa A. agaricites Colpophyllia	M. cavernosa Siderastrea
Common Species	Diploria Favia fragum Siderastrea	A. agaricites Dichoenia	Madracis Siderastrea	
Coral Cover	high cover	low cover	moderate cover	moderate to low
Diversity	low diversity	high diversity	moderate diversity	low diversity
Depth Range	0–6 meters	5–10 meters	9–24 meters	22 to 40+ meters
Comments		very abundant, octocoral, almost a hard ground	coral spurs alternate with sediment grooves	rocky surface, very little sediment cover
	low slope, almost a terrace	drop-off area with fairly steep slope	fairly high slope	
	dominated by branching coral	scattered, small heads, still abund. branching	massive, interlocking heads	platy, fragile forms, isolated heads

terrace level. Abundant octocorals and soft organisms are associated with this zone, and in places the assemblage approaches a hardground facies.

A break in slope generally occurs between the Mixed Coral Zone and the Massive Coral Zone. Coral species in the massive zone grow on a relatively steep slope and are dominated by *Montastrea, Porites,* and *Agaricia* species (Table 2). The data in Table 2 allow statistical comparisons between the different reef transects. The upper part of the zone terminates at 12 to 14 m on the emergent reefs and the lower part of
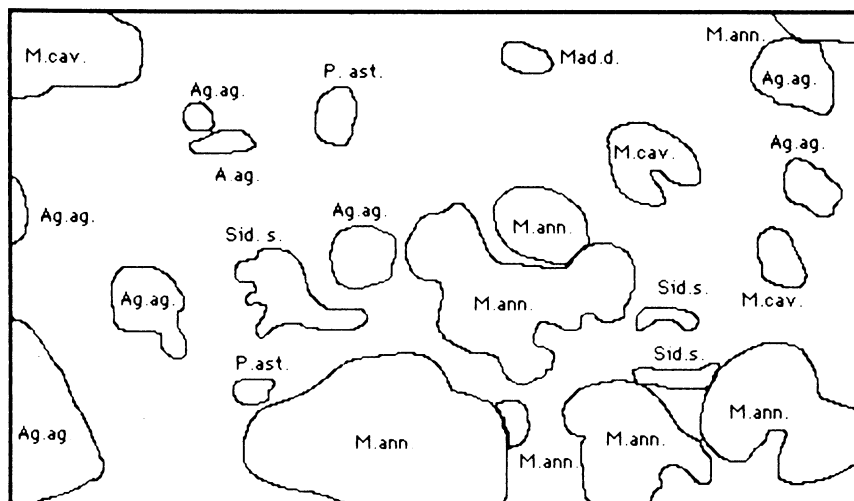
FIGURE 2—Coral reef transect photograph. Living coral are outlined in ink, and the species is identified in the field and noted by tag number.

PONCE SEDIMENTS

Four reef sites were surveyed at Ponce (Fig. 4). These sites at Bajo Tasmanian, Cayo Cardona, Cayo Ratones, and Peñuelas Reef are successively farther from the Ponce basin where a sediment plume is frequently formed by wave action resuspension of bottom sediments. This plume drifts westward over Bajo Tasmanian and Cayo Cardona reefs, and a remnant of the plume moves less often over the Ratones reef area. The plume has moved inshore or dissipated before it reaches the area of Peñuelas reef. No specific studies or measurements were made in the plume, but it has been observed and traced by the authors numerous times during the past five years.

A reef generates a volume of sediments at least equal to the mass of its growth (Hubbard, 1986). These sediments are transported away from the reef and coral continues to grow. When the pattern is affected by additional sediments from an outside source, coral growth can be inhibited or terminated. The amount of sediment reaching a reef can be measured by sediment traps and analysis of suspended sediments in the water column. We mapped the sediment facies and analyzed sediments collected on the reefs.

Sediment accumulation and subsequent resuspension are functions of sediment sources, wave and current energies, and bathymetry. Since the nature of sediments, and the amount of terrigenous sediment available is important to the discussions of this paper, we mapped the sediment types west of the area described by Beach (1975) (Figure 5).

The seaward shelf/slope unit at Ponce is the submerged shelf-edge reef system of living coral which forms the shelf-slope break and extends down the slope. The shelf breaks at 20 to 25 m depth. The reef may be a single or double ridge as described by Beach (1975). The sediments are consolidated reef rock and thin patches of carbonate sands. Off Isla Ratones, pockets of fine-grained terrigenous sediment are found below 15 m.

The carbonate platform sediments are shoreward from the shelf-edge reef system. This is an area of hard carbonate

the reef front forms a sand and gravel fore-reef talus zone on Enrique and Turrumote reefs. The lower part of the massive zone was measured at the submerged reef southeast of Turrumote reef and at the submerged shelf-edge reef (Figure 3). An overlap of the measured depths at the sites makes it possible to account for the effects of change in environments among the sites.

At 22 to 24 m, the composition of the reef community on the insular slope changes and the *Montastrea-Agaricia* coral zone can be distinguished. This zone was first described at Alacrán reef, México (Logan, 1969) and in Puerto Rico by Morelock et al. (1979) and Boulon (1979). *Agaricia* species and *Montastrea annularis* dominate the zone. Colony morphology changes from the massive rounded heads found in the shallower zones to platy forms.

TABLE 2—Diversity and coral cover by species at Parguera

Location	Depth	% Tot. Cov.	No. Sps.	Mna	Mnc	Aga	Agl	Pra	Sds	Mem	Cln	Dps	Dpc	Dpl	Stm	Mad	Myf	Myl	Acc
Buoy Shelf Edge	20	43.2	21	24.0	3.0	7.0		3.0	0.8	1.0	2.0	0.7	t	0.6	0.2	0.1	0.2	0.2	
Buoy Shelf Edge	25	49.0	28	26.0	2.2	15.2	.1	3.0	0.4	0.7	t^2	t	0.1	0.4	0.1	0.1	0.3	0.2	
Buoy Shelf Edge	30	40.7	19	14.7	2.7	14.0	4.4	2.0	0.2	0.3		0.4	0.2	0.3	0.1	0.2	0.3	0.2	
Turromote SE	15	15.7	13	6.5	2.4	2.0		1.0	1.1	0.4	1.0	0.1	0.1	0.7				0.1	0.1
Turromote SE	20	20.8	14	4.9	8.0	3.5		1.5	1.0	0.6	0.4	0.2		0.5	0.1	0.1		0.1	0.2
Turromote	5.0	6.8	8	0.5				2.2	0.3			0.8	t		t				0.6
Turromote	10	21.7	18	9.9	2.2	2.1		0.4	1.6	0.1	2.2	t			0.2	0.1		0.3	1.8
Enrique west	5.0	25.0	12	18.0	t	0.7		0.4	0.6		1.4							0.2	0.1
Enrique west	10	24.1	16	3.9	1.3	9.5		0.7	1.4	0.1	2.0				0.1	0.1		0.1	4.6

[1]Species abbreviations: *Mna* = *Montastrea annularis; Mnc* = *Montastrea cavernosa; Aga* = *Agaricia agaricites; Agl* = *Agaricia lamarcki; Pra* = *Porites asteroides; Sds* = *Siderastrea siderea; Mem* = *Meandrina meandrites; Cln* = *Colpophyllia natans; Dps* = *Diploria strigosa; Dpl* = *D. labrynthiformis; Stm* = *Stephanocoea mich; Mad* = *Madracis decactis; Myf* = *Mycetophyllia ferox; Myl* = *M. Lamarckii; Acc* = *Acropora cervicornis.*
[2]Trace

FIGURE 3—Shelf-edge break in massive coral zone. The shelf slope is 43 degrees.

pavement with thin carbonate sands and small reefs. The platform reefs have fair coral growth under conditions of moderate to strong currents and variable turbidity. Sediments are present in small channels.

The Ponce Basin extends to about 3 km west of Ponce Harbor and grades northward into the nearshore zone. Water depths are 12 to 34 m. The water is generally turbid with Secchi disc readings of less than 5 m. Sediments in the Ponce Basin are poorly sorted terrigenous silts and clays with small amounts of carbonate mud and sand that have been carried in from surrounding areas and have accumulated in low-energy, deeper-water conditions. Similar sediments floor the Ponce Submarine Canyon. The northern part of the basin is dominated by dark to olive terrigenous muds. Beach (1975) measured 65 to 70 cm of mud lying over a calcareous sand, showing a change in the depositional environment. He measured sediment accumulation on an artificial reef near Ponce to get an accumulation rate of 4 mm per year for the terrigenous muds. Applying this rate to the accumulated mud blanket shows that it could have been deposited during the last 125 to 150 years. Land stripping for sugar cane, urbanization, and dredging for harbor facilities could account for increased erosion and the development of this mud accumulation.

These fine sediments are resuspended by wave action and ship traffic. The resulting underwater visibility can be less than 1 m (pers. obs.). The resuspension develops a sediment plume that is transported by currents, carrying fine sediments over the reefs within and west of the basin. The nearshore province sediments are dark, fine-grained sand to fine-grained terrigenous muds. Moderate to strong longshore drift was observed.

Analysis of sediments collected at the four transect sites showed that the samples from depths of the five meter transects were dominantly sands, due to wave action removal of the fine fraction. Deeper parts of the reef had more fine-grained terrigenous sediments. Bajo Tasmanian and Cardona reefs had large amounts of fine-grained terrigenous sediments and poor sediment sorting. Both areas showed finer grain size and more terrigenous sediments at 15 m, suggesting that wave energy removes some of the terrigenous fines at depths above 10
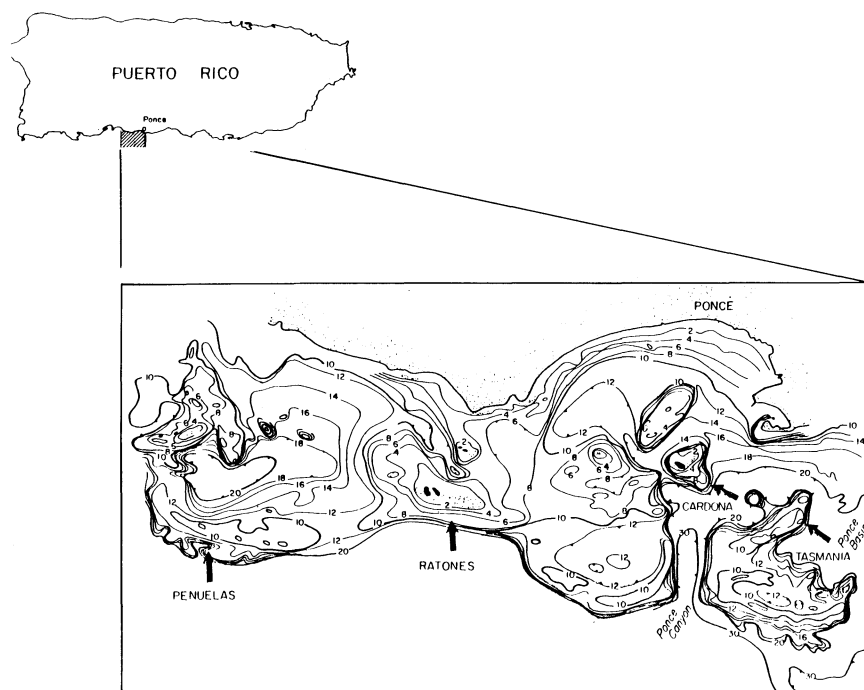
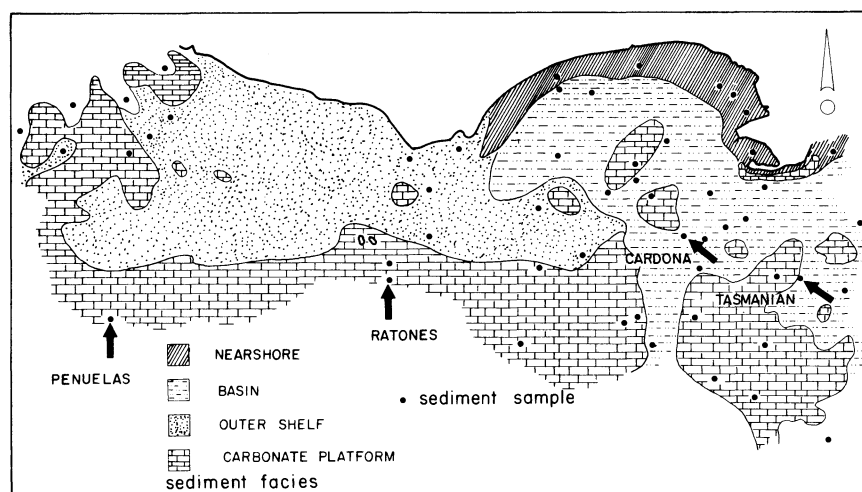FIGURE 4—Ponce shelf bathymetry and reef survey sites.

FIGURE 5—Ponce sediment facies and sample locations.
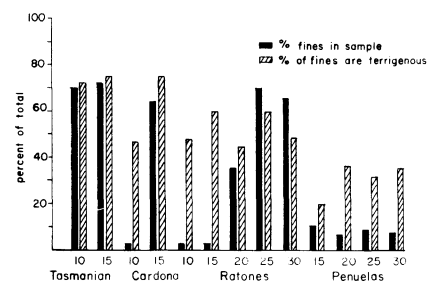

FIGURE 6—Percent of fine-grained sediments (< 0.063 mm in diameter in sediments accumulating on Ponce reefs. The second bar is the percent of these fines that are terrigenous.
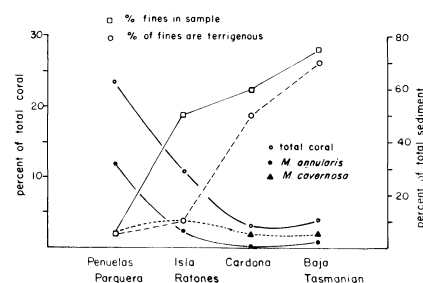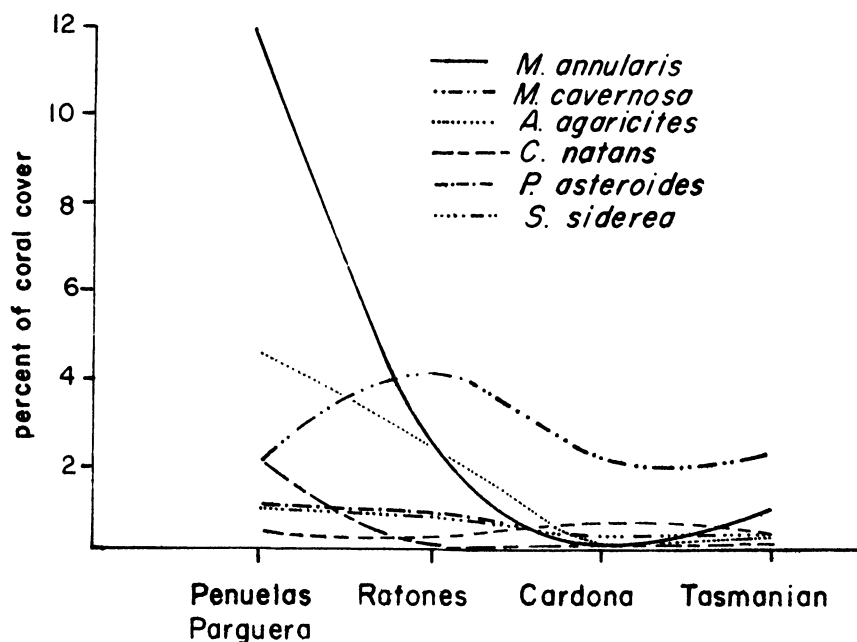

FIGURE 7—Percent of coral cover on Ponce reefs and percent fine sediments accumulating on the reefs.

m (Fig. 6). Cayo Ratones also showed an increase in fine terrigenous sediments with depth. The reef at Peñuelas had sand-size carbonate sediments even in the deeper parts of the reef (Acevedo, 1986); probably very little terrigenous sediment reaches this area, which is farthest downstream from the terrigenous sediment source.

PONCE REEF ZONATION

The coral cover and diversity on Bajo Tasmanian and Cayo Cardona reefs are severely modified by chronic sediment stress (Table 3). The percent total coral cover is drastically reduced at each equivalent depth in relation to the other reefs and *Montastrea cavernosa* dominates the coral cover. This coral is one of the most sediment-resistant species of the scleractinian corals (Lasker, 1980; Loya, 1976). The total cover of *Montastrea cavernosa* is not significantly different from values at La Parguera, but the reduction or absence of other coral species changes the relative abundance and reinforces the conclusion that *Montastrea cavernosa* is highly tolerant to a long-term sediment stress condition (Figure 7). One of the least sediment-tolerant species, *Acropora palmata,* was not present and is largely absent on reefs with high sediment influx (Morelock et al., 1979). A deepwater coral, *Agaricia lamarcki,* was found at 15 m on Bajo Tasmanian, suggesting that the light levels were greatly reduced. No living corals were found below 12 m at Cayo Cardona, and

TABLE 3—Diversity and coral cover by species at Ponce

Location	Trans.	Total	n.sp.	Mna	Mnc	Aga	Agl	Pra	Sds	Mem	Cln	Dps	Dpc	Dpl	Stm	Mad	Myf	Myl	Acc
									Species[1]										
B. Tasmanian	10 m	5.5	13	1.5	2.0	t^2		t	.5	.5	t	t					t		
B. Tasmanian	15 m	3.1	11	.2	1.8	.3	.1	t		.1					.2	t		.3	
Cardona	5 m	0.4	3						t			.1							
Cardona	10 m	3.6	11	.1	2.5	t		t	.1	.6		.3			t	t			
Ratones	5 m	6	9	2.3	t	.1		1.1	.3			.1			.1				
Ratones	10 m	9.5	14	1.6	4.1	1.6		1.0	.7	.2	t	.2	t	t	t	.2			
Ratones	15 m	12.5	11	3.3	3.4	2.9	.5	.7	.6	.3					t	.4		.4	
Ratones	20 m	6.7	13	.5	1.1	3.0	.6	t	.4	.1					t	.1	t		
Ratones	25 m	4.8	7			.4	3.9	.1	.2	t					.1	.1			
Ratones	30 m	0.1	2					t								t			
Peñuelas	15 m	28.7	17	16	2.1	3.4	.1	1.6	.4	.3	2.3	.2			.1	.2			.1
Peñuelas	20 m	24.1	16	10.7	2.1	6.2	.4	1.4	.9	.8	.3	.2	t		.2	.1		.1	
Peñuelas	25 m	17.7	18	2.7	1.7	8.2	.4	.6	.5	.9		.3			.9	.2		.8	
Peñuelas	30 m	8.1	11	.1	.5	3.4	3.8		.1	.1					t	.1			

[1]See Table 2 for abbreviations.
[2] Trace

FIGURE 8—Percent of cover by coral species on Ponce reefs.

dead coral heads were covered with a sediment-algae mat.

Cayo Ratones showed changes in coral cover related to sediment stress, but much less than at Cardona. Coral cover and species diversity were higher compared to Bajo Tasmanian and Cayo Cardona, but deeper parts of the reef were affected by terrigenous sedimentation. Above 15 m, the effects were less and the reef was more like Peñuelas or Parguera reefs than the extremely changed reefs at Cardona and Bajo Tasmanian. Below 15 m, the wave action on the south coast does not remove all the fine sediments. The combination of depth and turbidity causes greater light reduction than found at an equivalent depth at Parguera. *Montastrea cavernosa* was dominant at 10 m and important at 15 m. A platy coral assemblage was dominant below 15 m. A hummocky topography was formed by dead coral heads covered with the sediment-algae mat. At 25 m only four coral species were present in appreciable amounts, with only *Agaricia lamarcki* common. Only two species (*Agaricia lamarcki* and *Madracis decactis*) were found at 30 m.

Peñuelas reef was very similar to the Parguera shelf edge reef in terms of coral distribution patterns and coral species diversity. Coral cover was higher at La Parguera for the 25 and 30 m depths, but this was attributed to minor differences in water transparency.

OBSERVED SEDIMENT EFFECTS ON PONCE REEFS

In the reefs of Puerto Rico, two effects of sediment stress seem to be especially important. The development of an algal-sediment mat over dead coral surfaces limits space for recolonization or advancement of a coral colony.

TABLE 4—Total coral cover and number of species (diversities).

Reef & Percent Coral Cover	DEPTH (m)					
	5	10	15	20	25	30
Parguera shelf edge	—	—	—	43	50	51
Turromote southeast	—	—	16	21	—	—
Turromote	7	22	—	—	—	—
Enrique	25	24	—	—	—	—
Peñuelas shelf edge	—	—	29	24	18	8
Ratones	6	10	13	7	5	0.1
Cardona	0.1	4	0	—	—	—
Bajo Tasmanian	—	6	3	—	—	—
Reef & Number of Species						
Parguera shelf edge	—	—	—	21	20	19
Turromote southeast	—	—	12	14	—	—
Turromote	8	18	—	—	—	—
Enrique	13	16	—	—	—	—
Peñuelas shelf edge	—	—	17	16	18	11
Ratones	9	14	13	11	7	2
Cardona	3	9	0	—	—	—
Bajo Tasmanian	—	12	11	—	—	—
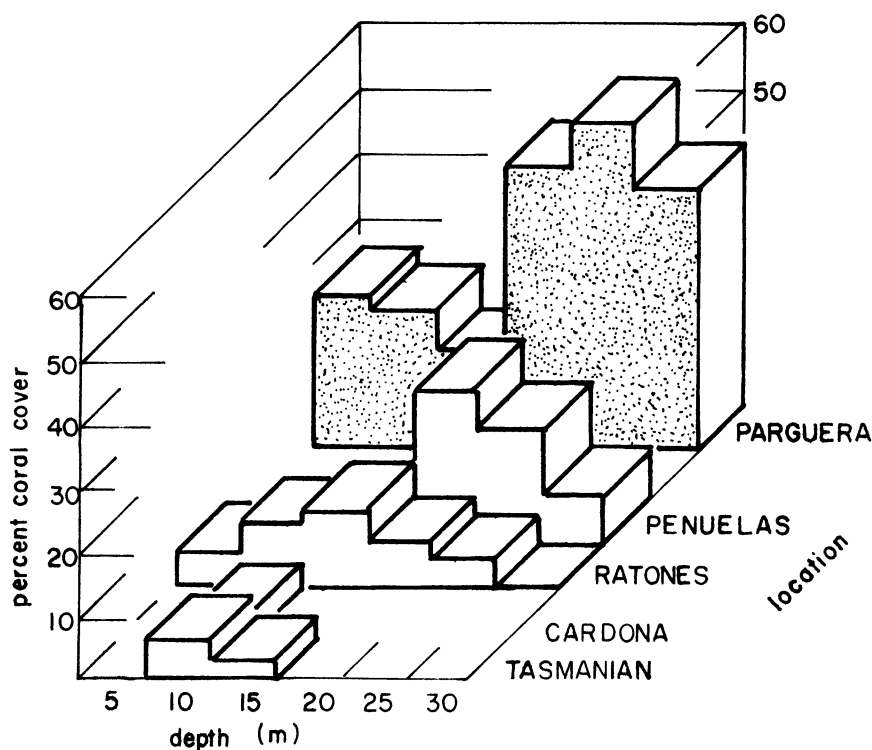
FIGURE 9—Percent of total living coral cover for all transects.

The influx of sediments and nutrients has shifted the balance of competition to algal growth. The mat can be seen to grow over living coral polyps, advancing at the expense of the coral. This shift is probably strongly influenced by the higher nutrient levels that are carried into the environment along with the fine-grained terrigenous sediments (see Hallock and Schlager, 1986, for discussion of nutrient effects).

Individual species of coral have resistance to sediment stress up to certain critical levels; these differences in tolerances were reported by Fisk (1981) and Rogers (1977). The sediment tolerance determinations were made by smothering or shading experiments and may differ from species resistances to a long period of sediment stress. The differences should be reflected in the ecology of a stressed reef, and are, to a certain extent. Morelock et al. (1979) found that the last surviving colonies in areas of high sediment were *Montastrea cavernosa, Siderastrea siderea, Agaricia agaricites,* and *Porites asteroides.* Cortés and Risk (1985) reported a shift to sediment-resistant species and platy coral morphology at shallow depths in sediment-impacted reefs at Cahuita, Costa Rica.

In our study, a maximum of 18 species of corals were recorded at 10 to 15 m depth. Of these, only 7 species were more than 0.5 % cover (not percent of cover) on any reef. We pooled the 10 and 15 m transects and examined the changes in coral cover by species with increased sediment influx (Fig. 8). The values for *Montastrea annularis* and *Agaricia agaricites* decreased significantly with increased sediment conditions. The main loss in total cover was reduction in cover by *Montastrea annularis*. The cover by *Montastrea cavernosa, Siderastrea siderea, Porites asteroides, Colpophyllia natans,* and *Meandrina meandrites* was not significantly different between sites.

Coral cover was reduced near the source of terrigenous sediment influx and coral cover and number of species increased with distance from the Ponce Basin. Reduced amounts of sediment trapped on reefs distant from the Ponce Basin suggest that the plume influx accelerated the deterioration of nearby reefs. Because Bajo Tasmanian had more coral cover and species diversity than Cayo Cardona, additional resuspension of bottom sediments by ship traffic may have added to the sediment stress. The Ponce reefs affected by terrigenous sediments showed decreased coral cover (Fig. 8), lower species diversity, and reduced vertical zonation compared to La Parguera reefs (Table 4).

The depth at which living coral can be found is directly related to clarity of the water column. Reefs at Belize and Jamaica have living coral to more than 100 m and at La Parguera shelf edge, living coral was observed past 70 m. The deepest living coral at Peñuelas was at 60 m and at Ratones no coral was observed below 32 m. At Bajo Tasmanian no coral was found below 18 m and the lower limit of living coral at Cayo Cardona was 12 m. The shelf edge reefs at Peñuelas and La Parguera were relatively free of terrigenous sedimentation; species richness and coral cover values compared favorably with other Caribbean reefs.

The most striking and important effect of the terrigenous sediment influx is the increased turbidity and loss of light, which results in shifting of the zonation and an upward migration of zone depths (Hallock and Schlager, 1986). Loss of light is critical to the deeper coral assemblages, and a chronic increase in turbidity will move the lower limit of coral growth to shallower depths. This is reflected by a marked change in the reef-front zonation with depth. A compression of the depth zonation is accompanied by changes in coral species domination, which is directly related to individual species tolerances for sediment stress. Both loss in total coral cover and a shift to slower growing coral species were seen.

Comparison of the changes at Cardona, Bajo Tasmanian, and Ratones to the deeper levels at Peñuelas and La Parguera also showed an absence of many species that normally extend to depths of 25 or 30 m. Tolerance of individual species to sediment particles is probably another factor in the final coral species assemblage. Continued stress has reduced the total cover and the number of species from more than 20 to less than 5. The reefs with high sediment input showed decreased coral species diversity and percent cover. Sediment-resistant species tolerated this adverse environment and their percent cover remained relatively constant. The results from sediment influx commonly seen were: partial or total burial of coral colonies, bleaching, colonization of the coral surface by filamentous blue-green algae and by sponges. The reduced light levels resulted in domination of the community by deeper fore-reef coral.

Recovery from sediment stress depends on the type and duration of the stress. The loss of the coral community and rapid loss of substrate as other organisms colonize and as algal-sediment mats develop, reduce the chance of recovery. The ecological conditions that follow the loss of a reef may be so different from those extant when the reef community developed that recolonization may be impossible.

ACKNOWLEDGMENTS

REFERENCES

BEACH, D.K., 1975, Sedimentation on the Western Isla Caja de Muertos Insular Shelf, Puerto Rico [unpub. M.S. thesis]: University of Puerto Rico, Mayaguez, Puerto Rico, 100 p.

BOULON, R.H., JR., 1979, Patterns of coral community structure and species diversity of a submerged shelf-edge reef off southwestern Puerto Rico [unpub. M.S. thesis]: University of Puerto Rico, Mayaguez, Puerto Rico, 61 p.

CORTÉS, J.N., and RISK, M.J., 1985, A reef under siltation stress: Cahuita, Costa Rica: Bulletin of Marine Science, v. 36, p. 339–356.

FISK, D.A., 1981, Sediment shedding and particulate feeding in two free-living sediment dwelling corals (*Heteropsammia cochlea* and *Heterocyathus aequicostotus*) at Wistari Reef, Great Barrier Reef: Proceedings 4th International Coral Symposium, v. 2, p. 21–25.

GOREAU, T.F., and GOREAU, N.I., 1973, The ecology of Jamaican coral reefs Part II. Geomorphology, zonation, and sedimentary phases: Bulletin of Marine Science, v. 23, p. 399–464.

HALLOCK, P., and SCHLAGER, W., 1986, Nutrient excess and the demise of coral reefs and carbonate platforms: PALAIOS, v. 1, p. 389–398.

HUBBARD, D.K., 1986, Sedimentation as a control of reef development: St. Croix, U.S.V.I.: Coral Reefs, v. 5, p. 117–125.

JAMES, N.P., and GINSBURG, R.N., 1979, The morphology, sediments and organisms of the deep barrier reef and fore-reef: *in* JAMES, N.P., and GINSBURG, R.N., eds., The Seaward Margin of Belize Barrier and Atoll Reef: International Association of Sedimentologists Special Publication No. 3, Blackwell Scientific Publications, Oxford, London, p. 25–64.

LASKER, H.R., 1980, Sediment rejection by reef corals: The roles of behavior and morphology in *Montastrea cavernosa:* Journal of Experimental Marine Biology and Ecology, v. 47, p. 1158–1159.

LOGAN, B.W., 1969, Carbonate sediments and reefs, Yucatan Shelf, Mexico. Part II. Coral Reefs and Banks: American Association of Petroleum Geologists Memoir 11, p. 131–198.

LOYA, Y., 1976, Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals: Bulletin of Marine Science, v. 26, p. 450–466.

MORELOCK, J., BOULON, K., and GALLER, G., 1979, Sediment stress and coral reefs: *in* LOPEZ, J.M., ed., Symposium of Energy Industry and the Marine Environment in Guayanilla Bay: Center for Energy and

Environment Research, Univ. of Puerto
Rico, Mayaguez, Puerto Rico, p. 46–58.

MORELOCK, J., SCHNEIDERMANN, N., and BRY-
ANT, W.R., 1977, Shelf reefs, Southwest-
ern Puerto Rico: *in* FROST, S.H., WEISS,

M.P., and SAUNDERS, J.B., eds., Reefs and
Related Carbonates—Ecology and Sedi-
mentology, Studies in Geology No. 4,
American Association of Petroleum Geolo-
gists, Tulsa, Oklahoma, p. 17–28.

ROGERS, C.S., 1977, The response of a coral
reef to sedimentation [unpub. Ph.D. the-
sis]: University of Florida, Gainesville, FL,
196 p.